The Role of Increased Sea Surface Temperature on Eelgrass Leaf Dynamics: Onset of El Niño as a Proxy for Global Climate Change in San Quintín Bay, Baja California

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Abstract.—We present a quantitative study of the effects of sea surface temperatures on eelgrass productivity variables. We compared standing stock variables for *Zostera marina* for the strong El Niño event of 1986–1987, previously published by other workers for San Quintín Bay, Baja California, to our previously unpublished data for the "normal year" of 1992–1993. We found significant differences for most of the variables measured, which included Leaf Area Index, leaf length, width, dry weight and area, biomass, shoot density, and number of leaves per shoot. Inspection of the multivariate ENSO index (MEI) and sea surface temperature (SST) anomalies for each of these years showed that the differences could be explained by the warm SSTs associated with the ENSO event. We were able to explain the observed differences from a dynamic perspective by using a leaf-growth model forced by SSTs. We conclude that sea surface temperature summarizes the fundamental environmental influences on eelgrass leaf dynamics observed in our study site. That is, higher SSTs explain the reduction in mean leaf lengths and the corresponding diminution in related productivity variables. This study also strengthens the view that the onset of an El Niño event provides anticipatory evidence for the effects that a rise in global temperature is expected to elicit in eelgrass beds.

Human-induced increases in atmospheric concentrations of greenhouse gases are expected to exacerbate global temperature change (Ramanathan 1988). The associated alterations could be particularly deleterious for estuaries and coral reefs, currently under noticeable anthropogenic stress. These relatively shallow environments will be affected through alterations in abiotic variables like temperature and sea level, wind patterns and storminess, availability of precipitation water and runoff, and modifications in availability of nutrients (Dyer 1985; Emanuel 1987; Wigley and Raper 1987; Bakum 1990; Peterson *et al.* 1993; Watson et al 1996; Kennedy et al. 2002).

Sea-surface temperature has been found to have a great influence in marine ecosystem dynamics (Tegner and Dayton 1987; Baumgartner *et al.* 1992; Beer and Koch, 1996; Holbrook et al. 1997; Johnson et al. 2003). In particular, warmer

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temperatures are expected to influence the biology of organisms by reducing the concentration of dissolved oxygen in seawater. Diurnal and annual temperature oscillations also influence the biology and distribution of aquatic angiosperms (Holmes & Klein, 1987). Several workers have reported that growth dynamics of the temperate seagrass *Zostera marina* L. is highly correlated with sea surface temperature (Short an Neckles 1999; Solana-Arellano *et al.* 1997, Poumian-Tapia & Ibarra-Obando 1999; Solana-Arellano et al. 2004). According to Setchel (1929) eelgrass can grow only within a fixed temperature range. Other authors (Rasmussen 1977; Phillips and Backman 1983) have also shown that temperature is fundamentally important in controlling the seasonal growth cycle of eelgrass.

The distribution and abundance of seagrasses in temperate littoral waters are also controlled by light availability (Backman and Barilotti 1976; Denninson and Alberte 1985; Bulthuis and Woelkerling 1983; Orth and Moore 1988; Zimmerman *et al* 1991). In particular, light has been shown to influence the distribution (Dennison & Alberte 1985), density (Mukai et al. 1980), flowering (Phillips & Backman 1983), biomass (Mukai et al. 1980) and production (Bulthuis 1987) of *Zostera marina*.

Dissolved oxygen, inorganic nutrients (including carbon) and water movements also modify photosynthesis in aquatic plants. While light, temperature and dissolved oxygen regulate instantaneous photosynthetic rates, the availability of inorganic nutrients affects the long-term response of photosynthesis by controlling the levels of photosynthetic enzymes and pigments (Solana-Arellano et al. 1997). Eelgrass can absorb nutrients either from the roots or the leaves (McRoy et al. 1972). Hence, modifications in upwelling activity, stratification, and tidal dynamics could alter the availability of dissolved nutrients and thus affect seagrass productivity. In our study area (San Quintin Bay, Baja California, one of the last remaining ecologically functional estuaries in the California Bight), the onset of an ENSO event alters sea surface levels and temperatures, as well as tidal dynamics and nutrient availability (Álvarez-Borrego 2004). Hence, it is reasonable to expect that ENSO-like conditions would influence eelgrass dynamics in the bay. Sea surface temperature provides a reasonable paradigm for an ENSO-like alteration. Since thermal expansion of the water column influences sea level variation (Wigley and Rapper 1987) sea level can be assumed to increase, thus modifying light availability and changing tidal dynamics and circulation (Short and Neckles 1999). Also, thermally induced stratification would imply a deeper thermocline and nutricline, and modify upwelling transport of dissolved nutrients (Petterson et al. 1993). Hence we would expect sea surface temperature to be a variable that triggers changes in the dynamics of the principal environmental influences on eelgrass in our study site.

To provide a basis for the assumption of significant causal linkage between an ENSO warming event and changes in the growth dynamics of eelgrass we demonstrate here that sea surface temperature accounts in a fundamental way for the observed variability of standing stock variables by comparing two whole-year-cycle data sets of *Z. marina* L. in the San Quintín Bay estuary. The first data set, for the ENSO event of 1987–1988, was previously published by Ibarra-Obando et al. (1997). The second data set was collected by our research group from November 1992 through November 1993. Both data sets consist of means for leaf

length, width, dry weight and area, biomass and density per square meter, Leaf Area Index (LAI), and number of leaves per shoot.

Due to the architecture of Z. *marina*, above-ground productivity is determined by the dynamics of leaf elongation. To show that temperature controls productivity, we demonstrate a causal relationship between temperature and leaf length by using a leaf-growth model forced by sea surface temperature. We produced a consistent representation of leaf-length dynamics for both data sets and corroborated that sea surface temperature can be considered a fundamental environmental forcing agent for productivity variables of eelgrass at our study site. An alteration of the normal variation range for this variable like that registered during the onset of an ENSO event provides anticipatory evidence for the effects that an equivalent change in global temperature would elicit on eelgrass beds at our study site. This agrees with the view on this causal relationship for seasgrasses discussed in Short and Neckles (1999).

Study Site

San Quintin Bay is a Y-shaped shallow coastal lagoon on the Pacific side of the Baja California Peninsula, Mexico (30°30N–116°10′W), which has a total area of 42 km^2. Evaporation exceeds runoff plus precipitation. In the Bay's waters, tides are mixed and predominantly semidiurnal and are considered the main cause of temperature variability (Álvarez-Borrego 2004). Upwelling events bring nutrient-rich waters near the mouth of the bay (Dawson 1951) and tidal currents propagate those waters throughout the bay. To some extent, this accounts for the rather high nutrient content of its waters (Barnard 1962; Álvarez-Borrego and Álvarez-Borrego 1982). Organic matter is trapped and materials are re-mineralized, releasing nutrients back to the water column. These remineralization processes (Smith et al. 1991), along with turbulence induced by tidal currents and waves, control nutrient concentrations in the lagoon (Álvarez-Borrego 2004).

Sampling and Exploratory Analysis

The sampling site is a mudflat located in the west arm of the bay. We collected shoots monthly from sixteen 20 × 20 cm quadrats selected at random, from November 1992 through November 1993. Each sample was placed in individually labeled plastic bags and cooled until processed. Each shoot was cleaned with distilled water. We determined the number of shoots and leaves per unit area, the length (*mm*), width (*mm*) dry weight (*g*), and area (*mm*^{2}) of each leaf. A total of 10,000 complete leaves were collected through the entire year cycle. Biomass per unit area and L.A.I estimations are presented in *g m*$^{-2}$ and *m*^{2} *m*$^{-2}$ respectively. For both data sets that were analyzed, underwater radiation at 1 meter under sea level was measured (*Em*$^{-2}$) by using a PAR and direct beam quantum radiometer-photometer (Li-Cor, Inc.) using an integration time of 1000 s. The integrated photon flux rate in a time interval centered at noon gives a reasonable estimate of the maximum radiation in the day. Daily variation can then be approximated by the Monteith sine law (Monteith 1965). *In situ* temperatures for both data sets were also obtained (figure 5 b). Principal Component Analysis (PCA) was developed for all variables in both our data and that of Ibarra-Obando et al. *(*1997) to assess the importance of abiotic variables. Nutrient data are not available for 1992–1993 so we used upwelling index values as a proxy in accordance with

Álvarez-Borrego (2004) that reports upwelling as the main source of dissolved nutrient availability in the site.

Data in MEI values SST anomalies and Upwelling index were obtained from NOAA (http://www.cdc.noaa.gov.people.klauss.wolter/MEI/table.html, http://ferret.pmel.noaa.gov/NVODS/servlets/datasets and ftp://orpheus.pfge.noaa.gov/outgoing/upwell/monthly/upindex.mon). Data on sea level values at San Quintin Bay were provided by the Laboratorio de Nivel del mar, Departamento de Oceanografia Física CICESE (http://nivelmar.cicese.mx/).

Theoretical Methods

Following Nadezhda et al. (2001) we considered that water temperature, light radiation and nutrients are the fundamental environmental influences on eelgrass growth. In accordance with Álvarez-Borrego (2004) we will consider that the availability of dissolved nutrients is controlled by upwelling activity at our study site. We designate sea surface temperature by $T(t)$ at a time t. Similarly $\phi(t)$ means underwater light radiation and $U(t)$ are values of the upwelling index.

Let $l(t)$ denote eelgrass leaf length. Then, leaf length rate dynamics will be assumed to follow the growth model,

$$\frac{dl}{dt} = k(t)[l_\infty - l(t)], \tag{1}$$

where l_∞ is the maximum possible value that leaf length can be attain. This constant is also known as the asymptotic upper bound for leaf growth. For leaf length values that are very close to l_∞, vanishing leaf length rates are expected (Batschelet 1974). The scaling factor $k(t)$ summarizes the fundamental environmental influences on leaf dynamics. It can be formally represented through the expression

$$k(t) = f(T(t), \phi(t), U(t)), \tag{2}$$

where $f(t)$, $\phi(t)$, $U(t)$ is assumed to be continuous and differentiable in all of its arguments. Increasing water temperatures are known to affect eelgrass metabolism and the maintenance of a positive carbon balance (Zimmerman et al. 1989). Optimum eelgrass photosynthesis is attained at temperatures below a seasonal maximum (Biebl and McRoy 1971). Temperatures above the growth optimum to near the upper limit of thermal tolerance have resulted in reduced eelgrass productivity (Thayer et al. 1984; Moore et al. 1996). This conceptual framework, along with the assumption that a change in $T(t)$ triggers a response in the remaining variables of equation (2) is consistent with the assumption that $k(t)$ can be represented in terms of mean sea surface temperature $T(t)$. The forcing factor $k(t)$ can be assumed to have the polynomial form

$$k(t) = \sum_{n=1}^{N} a_n T^n(t). \tag{3}$$

Integration of equation (1) from t_i to t_{i+1} led us to the equation,

$$\frac{l_\infty - l(t_{i+1})}{l_\infty - l(t_i)} = \exp\left[\int_{t_i}^{t_{i+1}} k(t)\, dt\right] \tag{4}$$

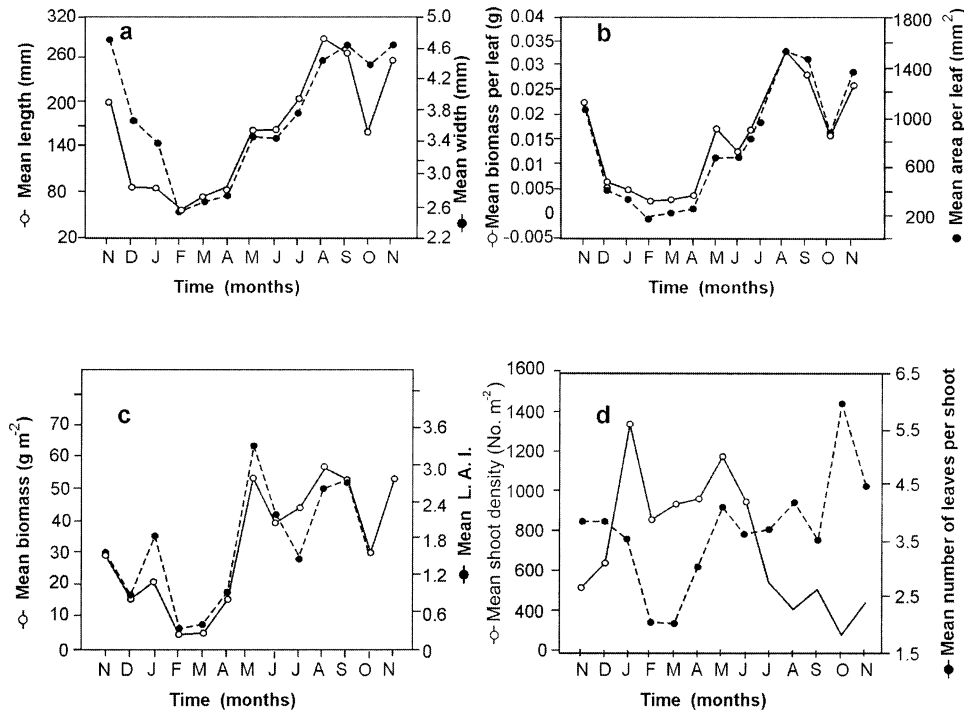After a few algebraic steps equation (4) provides the regression expression,

Fig. 1. Mean monthly values for *Zostera marina* standing stock variables and leaf area index (LAI) measured in San Quintin Bay during the "normal" year of 1992–1993.

$$l(t_{i+1}) = l_\infty - [l_\infty - l(t_i)]e^{G(t_i,t_{i+1})} \tag{5}$$

where by virtue of equation (3) $G(t_i, t_{i+1})$ has the form:

$$G(t_i, t_{i+1}) = -\sum_{j=1}^{N} a_i \int_{t_i}^{t_{i+1}} T^i(t) \, dt \tag{6}$$

In order to corroborate empirically the assumption of equation (3) we fitted equation (5) to available data on leaf length and sea surface temperature. Determination coefficients, graphs of predicted *vs* observed values and residual analyses are presented in the results section. The mean square regression method and the statistical package STATISTICA were used in these fittings.

Results

Maximum leaf width was 4.6 mm and occurred in November 1992, and maximum leaf length of 290 mm was reached in August 1993 (Fig 1). Leaf-widths close to maximum values also occurred in September and November 1993. Changes in mean leaf length and width followed the same variation pattern; the maximum for both measurements was attained by late summer (Fig. 1a). Similar results were obtained for mean leaf area and mean leaf biomass; both measurements reached their maximum in August, (Fig. 1b), these were 1543 m m² and 0.*034* g respectively. Biomass per unit area reached a maximum of 57.02 g m⁻² in August, but another peak of 54.04 g m⁻² occurred in May (Fig. 1c). This was
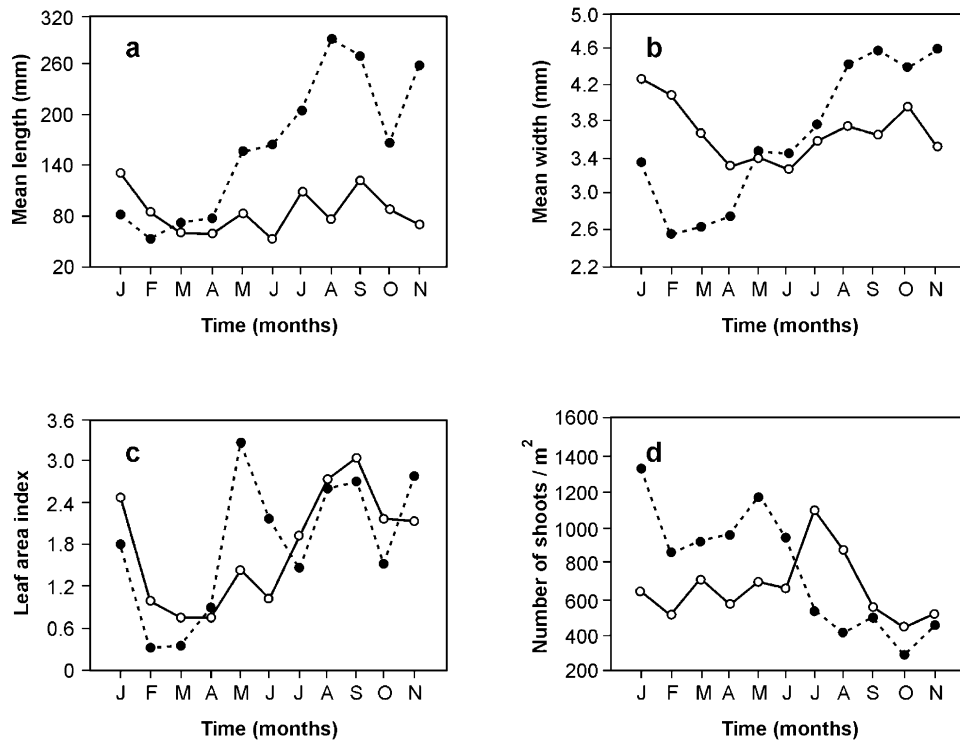
Fig. 2. Comparison of mean values for variables in our study with those of the 1986–1987 El Niño year reported by Ibarra-Obando et al. (1997) data at the same depth. Dashed lines corresponds to our study and continuous lines to Ibarra-Obando et al. (op. cit)

likely due to the period of reproduction, as a large number of reproductive shoots was observed at this time. Mean L.A.I had a maximum of 3.3 and was also attained in May. The inverse relationship between mean numbers of shoots and leaves is shown in Fig. 1d, such that minimum numbers of shoots (less than 400 shoots per square meter), occur when the number of leaves reaches its maximum of 6 leaves per shoot, and maximum number of shoots (1390 shoots m²) is reached almost at the same time the average number of leaves per shoot is declining to its minimum (2 leaves per shoot). This relationship could be explained by the autoecology of seagrasses (Kentula and McIntire, 1986), since light decreases during winter, the plant uses its energy to produce fewer shoots with a large number of leaves so they have more access to light.

For the El Niño year of 1986–1987, Poumian-Tapia & Ibarra-Obando (1999) reported smaller values for mean length, biomass, number of shoots and number of leaves per shoot than the ones found in our study for the same area (Fig 2.). We fitted a general linear model for upwelling index values in terms of dissolved nitrates and phosphates and their cross products, finding a determination coefficient of R^2 = 0.88. All estimated parameters had *p-values* < *0.05* (*0.0090* for nitrates, *0.009* for phosphates and *0.03* for the cross product of nitrates and phosphates), meaning that the 3 terms contribute to the multiple correlation coefficient. This result also provides a quantitative basis for the linkage between dissolved nutrient concentration and upwelling index values.

A Principal Components Analysis (PCA) for the 1987 data extracted a first component defined mainly by temperature, with a correlation coefficient of $R = 0.95$ and irradiance with a correlation coefficient of $R = -0.74$. This component explained 39% of the variability of biotic variables. Second and a third components were represented by nitrates and phosphates in that order, with coefficients of correlation $R = 0.91$ and $R = -0.66$ which explained 29% and 20% of the variability, respectively.

For the 1992–1993 data we used upwelling index values as a proxy for dissolved nutrient availability. In that PCA, we found a first principal abiotic factor defined by temperature and irradiance with correlation coefficient of $R = 0.85$ for temperature and -0.68 for irradiance. This factor explained 41.4% of the variability of biotic variables. A second component was mainly defined by upwelling with $R = 0.74$ and this factor explains 33.2% of the variability of all variables.

PCA results for both years, which showed a dominant forcing of SST on eelgrass productivity variables, were corroborated by the fittings of equation (5). This fitting produced a high coefficient of determination ($R^2 = 0.94$) for the 1987 data and an $R^2 = 0.97$ for the corresponding 1992–1993 leaf length data. Analysis of residuals showed a good correspondence between eelgrass leaf length and sea surface temperature for both data sets. Figure 3 shows the corresponding predicted *versus* observed values associated for each fit. This demonstrates that the observed differences can be explained by higher temperatures. In other words, sea surface temperature is a variable that summarizes the fundamental environmental influences that determine leaf length dynamics, and therefore of other variables such as biomass and L.A.I for eelgrass in our study site.

Discussion

This work presents the most recent data for important variables used in eelgrass production studies in San Quintin Bay (fig. 1). The nearest related sampling in the area occurred in 1987–1988, as reported by Ibarra-Obando et al. (1997). They reported smaller values for mean leaf length and also for most of the productivity related variables than our present results (fig. 2). An analysis of the causal linkage between sea surface temperature, underwater light radiation, dissolved nutrient availability and eelgrass productivity variables leads us to conclude that a higher temperature is the most important factor determining the observed differences. Our findings sustain the paradigm that a warm temperature stress can induce a deleterious effect in *Z. marina,* (Rasmusen, 1977, Penhale, 1977; Wetzel and Penhale, 1983; Evans et. al. 1986; Johnson et al. 2003).

Primary and secondary production in the California Current (CC) are high when the transport of the cool, low-salinity water from the north is strong and low when this transport is weak (McGowan 1983). Periods of warming and low productivity in the CC tend to coincide with El Nino events in the eastern tropical pacific. ENSO events induce warming of SSTs in San Quintin Bay (Silva-Cota and Alvarez-Borrego, 1988). The present analysis shows that slower growth rates in *Z. marina* reported by Ibarra-Obando et al. (1997) could be a consequence of the ENSO event that took place from June 1986 to January 1988, just before and during the year where their data were taken Comparison of MEI and SST values demonstrates clear differences between the 1987 ENSO and the ''normal'' conditions of 1993 (Fig 4.).
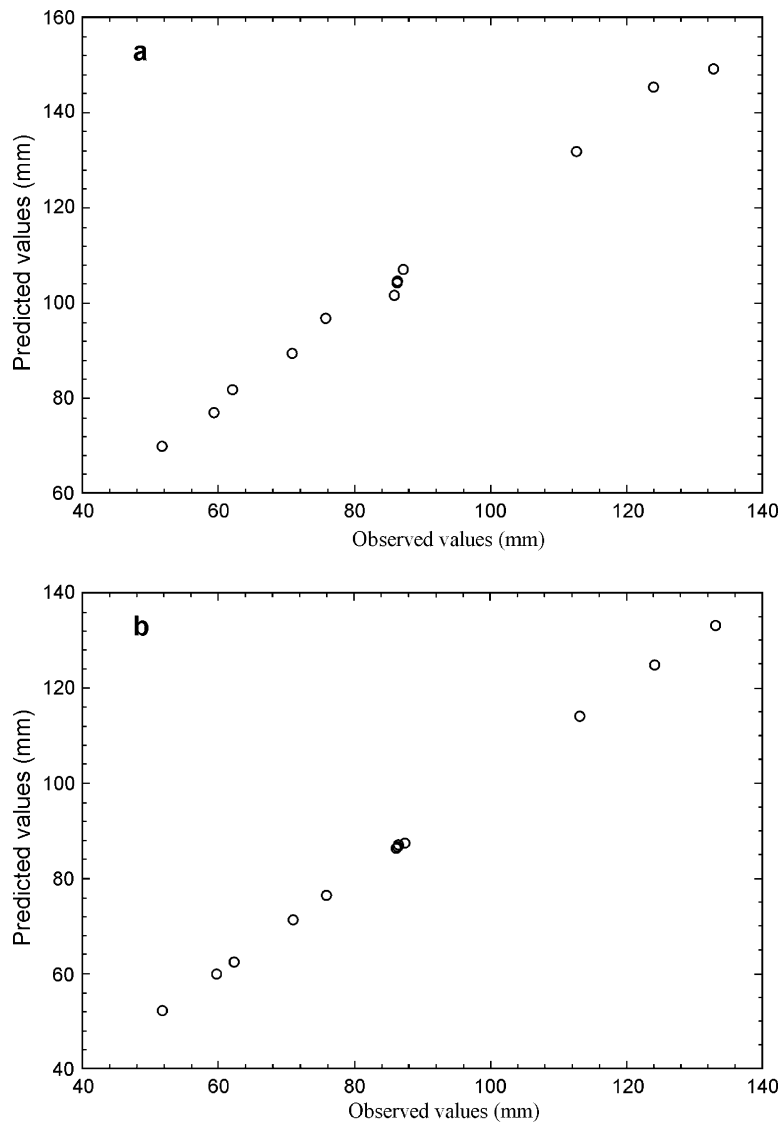
Fig. 3.   Observed versus predicted values for the fitting of equation (5) to mean length data. a) Fitting corresponding to the Ibarra-Obando et al. (1997) data. b) Fitting corresponding to our data.

Thermal expansion of sea water results in higher sea level values (Wigley and Rapper 1987), which can reduce light reaching seagrass beds at depth and thus limit photosynthesis (Short and Neckles (1999)). For *Z. marina,* the effects of decreased light are reduction in shoot density, leaf width, number of leaves per shoot, growth rate (Short *et al.* 1993) and above-ground plant productivity (Back- man and Barilotti 1976). Comparison of sea-level anomalies for San Quintín Bay, shows largely negative anomalies during the non-ENSO conditions of 1985 and positive anomalies during the 1987 ENSO (fig. 5). Thus we can infer that sea level anomalies were largely negative in 1993. There were also significant dif-
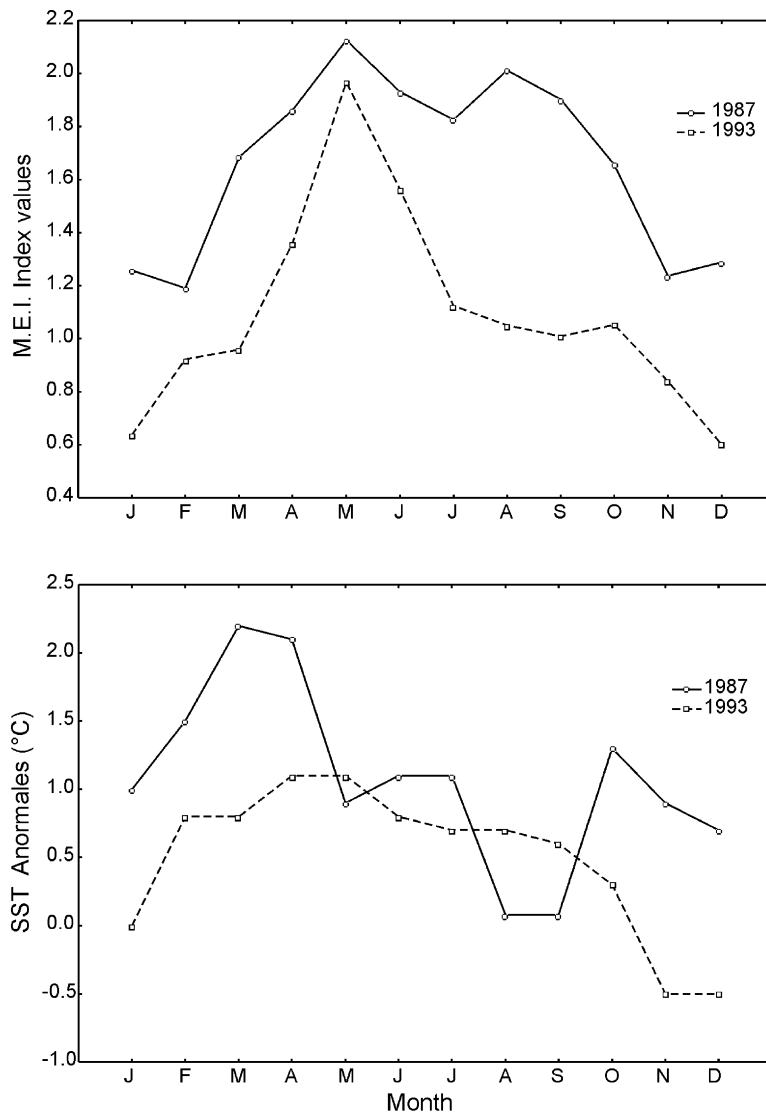
Fig. 4.   Above) Multivariate Enso Index values for 1987 and 1993. Below) Corresponding Sea Surface Temperature anomalies.

ferences (p = 0.03) in mean light radiation between our 1993 data and those of Ibarra-Obando (1997). This occurred for both the incident light flux and underwater light availability (Fig 6). Temperature stress and reduced availability of light likely contributed to lower productivity of eelgrasss in 1987.

Upwelling of nutrient-rich waters during non-ENSO conditions maintains high nutrient levels in the water column. But thermal stratification can modify the depth of both the thermocline and the nutricline and so influence nutrient transport by upwelling. Upwelling index values are in a good correspondence with dissolved nutrient availability, corroborating reports on the role of an ENSO event in the reduction of dissolved nutrient availability in our study site (Silva-Cota and Ál-
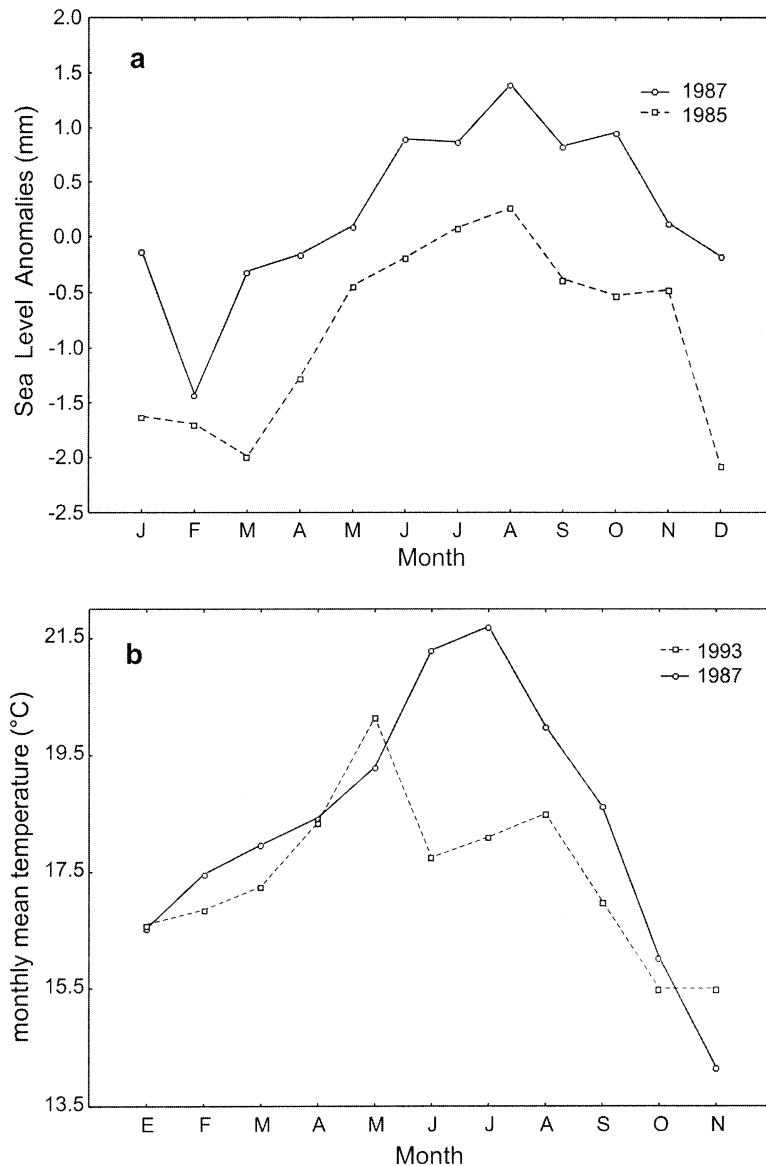
Fig. 5.   a) Sea level anomalies for San Quintin Bay for the ENSO year of 1987 and 1985 a year before the onset of the referred ENSO event. Higher sea level values for the ENSO event year area observed. b) Mean monthly temperatures for Ibarra-Obando et al. (1997) and present study data sets at San Quintin Bay.

varez-Borrego, 1988). This strongly suggests an unfavorable influence for eelgrass productivity, in addition to temperature and light availability effects.

We conclude that for the 1987 data the conjunction of a high temperature stress, reductions in light radiation and availability of dissolved nutrients could explain the diminution in eelgrass productivity variables during the 18-month ENSO event. Ibarra-Obando et al. (1997) found a turnover time of about 38 days for *Z.*
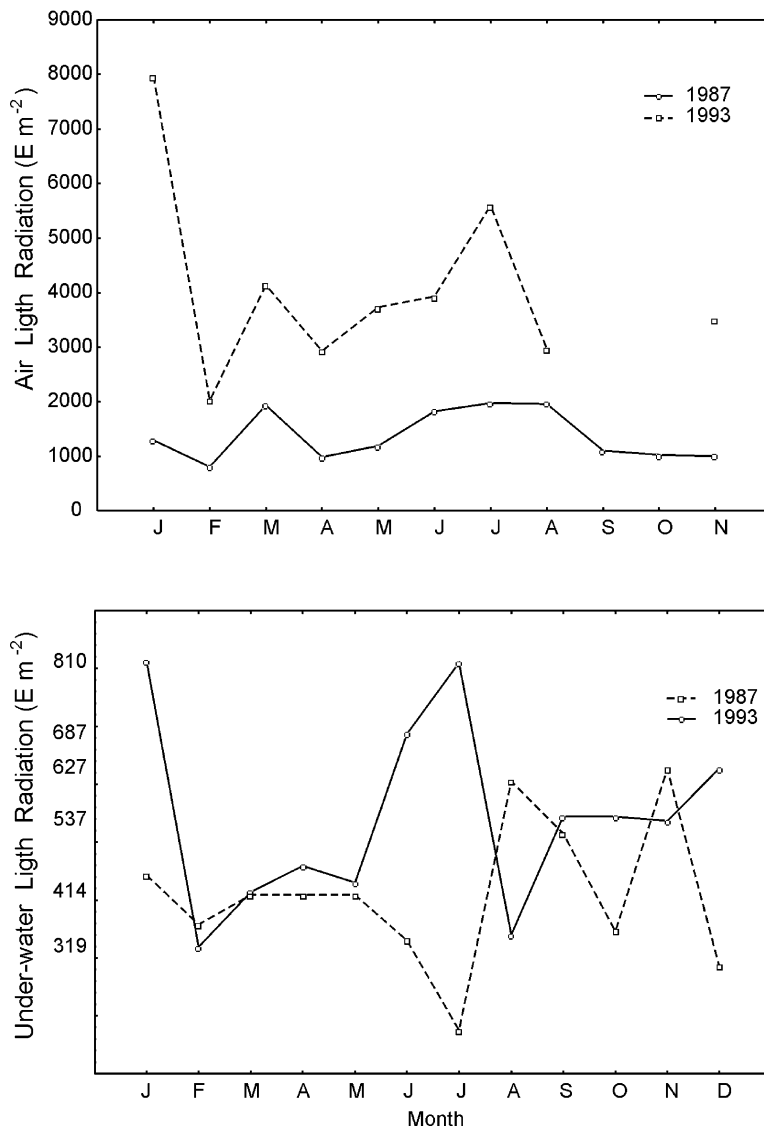
Fig. 6.   Above) Incident Light Radiation in San Quintin Bay during the ENSO event year of 1987 and 1993 which was consider as normal. Below) Underwater light luminosity corresponding to the same years. We can notice a grater light availability for the 1993 sampling period.

marina L., in San Quintin Bay. Reduced turnover times could have shortened responses to environmental stress for these seagrass populations in such a way that the associated effects were observable during the reported year–cycle study. In any event, both the performed PCA and the fitting of equation (5) show that environmental influences which controlled the observed dynamics can be summarized in a reasonable way by sea surface temperature variability.

The present study provides the first quantitative framework for corroborating the assumption that an increased temperature, as observed on the onset of an El

Niño event, will elicit reduced growth rates in *Z. marina* (Fig. 3). ENSO driven alterations are limited to 12–18 months between periods of normal conditions that range from 2–7 years. A continued ENSO–like anomaly could result in long-term unfavorable temperature conditions, triggering changes in light radiation and in the availability of dissolved nutrients. Besides the abatement of productivity variables, this could also disrupt adaptive response in eelgrass and promote its replacement by subdominant species as reported by Johnson et al. 2003.

Global climate change is expected to result in modifications of SST, sea level, CO_2 concentrations and UV radiation reaching the Earth's surface (Houghton and Woodwell, 1989; Mitchell 1989; Schneider 1994; Kerr 1992; Watson et al. 1996; Titus 1990; Smith et al. 1992; Schellnhuber et al. 2006), and to induce severe effects on both terrestrial and aquatic plants (Watson et al. 1996). In particular, global change is likely to exacerbate the deleterious effects of human activities on estuaries and costal lagoons (Kennedy *et al.* 2002). The effects of anthropogenic activities on estuaries are well documented in the literature (Roblee et al., 1991; Walker and McComb 1992; Short and Willie-Echeverria 1996). On the other hand the mechanism underlying climatic change effects are poorly understood. The expected changes linked to global warming on submerged plant species like sea grass beds and salt marshes are of a great concern due to the important ecological services they provide and the current extent of their loss.

The present study indicates that the onset of an El Niño event alters the San Quintin Bay environment with changes in sea-surface temperature, level and underwater light radiation. Similar changes for these variables are expected to occur in a global change scenario. Even though ENSO events have also driven changes in dissolved nutrient availability at the site, it is more difficult to predict how global change will affect this factor. Upwelling caused by northerly winds and the resulting offshore Eakman transport is a dominant oceanographic process in spring and summer along the entire California and Baja California Coast (Sverdrup et al. 1942). Observations show that wind-driven upwelling along the California Current has increased over the past 30 years (Snyder et al. 1993). This increase is assumed to be elicited by temperature gradients induced by increasing greenhouse gas forcing, but such association has been speculative. In the event of a positive association of global climatic change and intensification of upwelling, it might be reasonable to expect that the observed non-limiting nutrient environment within San Quintin Bay could be maintained. But increased sea temperature in the waters adjacent to the mouth of the bay and a coupled stratification could promote a deepening of the thermocline and nutricline, rendering upwelled waters deficient in nutrients, regardless of how intense the transport might be (Petterson et al. 1993). This coincides with reports on a reduced dissolved nutrient availability in the waters adjacent to the mouth of San Quintin Bay during an ENSO event (Silva-Cota and Álvarez-Borrego 1988).

Our findings strentengthen the view that the onset of an El Niño event provides valuable anticipatory scientific evidence on the effects on eelgrass productivity variables as a consequence of a global climatic change (Schneider 1994), particularly those associated with sea surface temperature, and underwater light radiation. For dissolved nutrients, the onset of an El Niño event at our study site could reduce dissolved nutrient availability probably linked to a deficient upwelling transport.

Acknowledgments

Literature Cited

Álvarez-Borrego J. and S. Álvarez-Borrego 1982. Temporal and spatial variability of temperature on two coastal lagoons., CalCOFI reports XXIII, 188–197.

Álvarez-Borrego S. 2004. Nutrient and phytoplankton dynamics in a coastal lagoon strongly affected by coastal upwelling. Ciencias Marinas, 30(1A)1–19.

Backman T.W. and D.C. Barilotti, 1976. Irradiance reduction effects on standing crops of the eelgrass *Zostera marina* in a coastal lagoon. Marine Biology, 34:33–40.

Bakum, A., 1990. Global climate and the intensification of coastal ocean upwelling, Science, 247: 198–201.

Barnard, J. L. 1962. Benthic marine exploration of San Quintin Bay California 1960–1961. Pac. Nat., 2:250–274.

Batschelet. E. 1974. Introduction to mathematics for life scientists. Springer Verlag New York. USA. 495 pp.

Baumgartner, T.R., A. Soutar and V. Ferreira-Bartrina 1992. Reconstruction of the history of Pacific sardine and northern anchovy populations over the past two millennia from sediments of the Santa Barbara Basin, California. CalCOFI Rep., 33: 24–40.

Beer, S. and E.W. Koch 1996. Photosynthesis of marine macroalgae and seagrasses in globally changing CO_2 environments. Marine Ecology Progress Series. 41: 199–204.

Biebl, R. and C.P. McRoy 1971. Plasmatic resistance and rate of respiration and photosynthesis of Zostera marina at different salinities and temperatures. Mar Biol. 8, 48–56.

Bulthuis, D.A. and W.J. Woelkerling 1983. Seasonal variations in standing crop, density and leaf growth of the seagrass *Heterozostera tasmanica,* in Western Port, Victoria, Australia. Aquatic Botany, 16: 111–136.

Bulthuis, D. A. 1987. Effects of temperature on photosynthesis and growth of seagrasses. Aquatic Botany, 27:31–50.

Dawson, E.Y. 1951. A further study of upwelling and associated vegetation along Pacific Baja California, México. Journal of Marine Research, 10:39–58.

Dennison, W.C. and R.S. Alberte. 1985. Role of daily light period in the depth distribution of *Zostera marina* L. (eelgrass). Marine Ecology Progress Series. 25: 51–61.

Dyer, K.R., 1995. Response of estuaries to climate change. In: Eisma, D. (Ed), Climate change: Impact on Coastal Habitation. CRC Press, Boca Raton. 85–110.

Emanuel, K.A., 1987. The dependence of hurricane intensity on climate. Nature, 326:483–485.

Evans, A.S., K.L. Webb and P.A. Penhale 1986. Photosynthetic temperature acclimation in two co-existing seagrasses, *Zostera marina* L. and *Ruppia maritima.* L. Aquatic Botany, 24:185–197.

Holbrook S.J., R.J. Schmitt and J.S. Stephens 1997. Changes in an assemblage of temperate reed fishes associated with a climate shift. Ecology Applications, 7: 1299–1310.

Holmes, M.J. and W.H. Klein 1987. The light and temperature environment. In: Plant life in Aquatic and Amphibious Habitats. Crawford, R. M. M. (ed) Blackwell Scientific Publications, Oxford 3–22.

Houghton, R.A. and G.M Woodwell 1989. Global climatic change. Scient. Am. 260, 36–44.

Ibarra-Obando S.E., C.F. Boudouresque and M. Roux 1997. Leaf Dynaics and production of a *Zostera marina* bed near its southern distributional limit. Aquatic Botany, 58:99–112.

Johnson M.R., S.L. Williams, C.H. Lieberman and Solbak, A., 2003. Changes in the abundance of the seagrasses *Zostera marina* L. (eelgrass) and *Ruppia maritima* L. (widgeongrass) in San Diego, California, following an El Niño event. Estuaries, 26: 106–115.

Kennedy V.S., R.R. Twilley, J.A. Kleypas, J.H. Cowan Jr. and S.R. Hare, 2002. Coastal marine ecosystems and global climate change: Potential effects on U.S. resources. Pew Center Report No. 8,52 pp.

Kentula M. and C. D. McIntire 1986. The Autoecology and Production of Eelgrass (*Zostera marina* L.) in Natarts Bay, Oregon. Estuaries, 9(3):188–199.

Kerr, R.A., 1992. Global change: Greenhouse science survives skeptics. Science 256, 1138–1140.

McGowan J. A. 1983. Biological effects of the 1983 Calofornian El Niño, paper presented at the annual CalCOFI Conference. Calif. Coop. Oceanic Fish Invest., Idyllwild, Calif.

McRoy C.P., M.J. Barsadate and M. Nebert 1972. Phosphorus cycling in an eelgrass (*Zostera marina* L.) Ecosystem. Limnology and Oceanography, 17:58–67.

Mitchell, J.F.B. 1989. The greenhouse effect and climate change. Rev. Geophy. 27, 115–139.

Monteith J.L. 1965. Light distribution and photosynthesis in field corps. Ann. of Bot. 29,17–37.

Moore K.A., Neckles, H.A. and R.J. Orth 1996. Zostera marina (eelgrass) growth and survival along a gradient of nutrients and turbidity in the lower Chesapeake Bay. Mar. Ecol. Prog. Ser. 142, 247–259.

Mukai H., K. Aioi and Y. Ishida 1980. Distribution and biomass of eelgrass (*Zostera marina* L.) and other seagrasses in Odawa Bay, central Japan. Aquatic Botany, 8:337–342.

Nadezhda Z., A. Sfriso, A. Voinov and B. Pavoni, 2001. A simulation model for the annual fluctuation of *Zostera marina* biomass in the Venice Lagoon. Aquatic Botany, 20:135–150.

Orth R.J. and K.A. Moore. 1988. Distribution of *Zostera marina* L. and *Ruppia maritima* L. sensu lato along depth gradients in the lower Chesapeake Bay, U.S.A. Aquatic Botany, 32: 291–305.

Penhale P.A. 1977. Macrophyte-epiphyte biomass and productivity in an eelgrass (*Zostera marina* L.) community. Jounal of Experimental Marine Biology and Ecology, 26: pp. 211–224.

Peterson C.H., R.T. Barber and G.A. Skilleter 1993. Global warming and coastal ecosystems response: How Northern and Southern hemispheres may differ in the Eastern Pacific ocean. In: H.A. Mooney, E.R. Fuentes and B. Kronberg (Eds). Early system response to global change: Contrast between North and South America. Academic Press NY. 17–34.

Phillips R.C. and T.W. Backman 1983. Phenology and reproductive biology of eelgrass (*Zostera marina* L.) at Bahía Kino, Sea of cortez México. Aquatic Botany, 17:85–90.

Poumian-Tapia M. and S.E. Ibarra-Obando. 1999. Demography and biomass of the seagrass *Zostera marina* in a Mexican Coastal Lagoon. Estuaries. 22(4) 837–847

Ramanathan V. 1988. The greenhouse theory of climate change: A test by inadverted global experiment. Science, 240:293–299.

Rasmussen E. 1977. The wasting disease of eelgrass (*Zostera marina*) and its effects on environmental factors and fauna. In: Seagrass ecosystems, a scientific perspective, C.P. McRoy & C. Helffrich, Marcel Dekker (ed), New York.

Roblee M.B., T.R. Barber, P.R. Carlson, M.J. Durako, J.W, Fourqurean, L.K. Muehlstein, D. Porter, L.A. Yarbro, R.T. Zieman, and J.C. Zieman. 1991. Mass mortality of the tropical seagrass Thalassia testudinum inFlorida Bay, (USA). Marine Ecology Progress Series 71: 297–299.

Schellnhuber H.J., W. Cramer, N. Nakicenovic, T. Wigley and G. Yohe. 2006. Avoiding dangerous climate change. Cambridge, U.K. 406 pp.

Schneider S.H. 1994. Detecting climatic change signals: Are there any fingerprints? Science 263, 341–347.

Setchel W. A. 1929. Morphological and phonological notes on *Zostera marina*. University of California Publications on Botany, 14:185–201.

Short F.T. 1987. Effects of sediment nutrients on seagrasses: Literature review and mesocosm experiment, Aquatic Botany 27:5547–555.

Short F.T., D. M. Burdick, J. Wolf, and G. E. Jones, 1993. Eelgrass in estuarine research reserve along the East Coast, USA. Part I: Decline from population and disease and Part II. Management of Eelgrass meadows. NOAA, Coastal Ocean Program Publication, 107 pp.

Short F.T. and S. Willie-Echeverria. 1996. Natural and human-induced disturbance of segrasses. Environmental conservation 23: 17–27.

Short, F.T. and H.A. Neckles. 1999. The effects of global climate change on seagrasses. Aquatic Botany, 63: 169–196.

Silva-Cota S. and S. Álvarez-Borrego 1988. The ''El Niño'' effect on the phytoplankton of a North-Western Baja California coastal lagoon. Estuarine Coastal and Shelf Sciences 27:109–115.

Smith R.C., B.B. Prezelin, K.S. Baker, R.R. Bidigare, N.P. Boucher, T. Coley, D. Karentz, S. MacIntyre, H. Matlick, D. Menzies, M. Ondrusek, Z. Wan, and K.J Waters, 1992. Ozone depletion: Ultraviolet radiation and phytoplankton biology in Antarctic waters. Science 255, 952–959.

Smith S.U., J.T. Hollibaugh, S.J. Dollar and S. Uimk 1991. Tomales Bay metabolism:C-N-P stoichiom-

ertry and ecosystem heterotrophy and the land-sea interface. Estuarine Coastal and Shelf Science, 33:223–257.

Snyder M. A., L.C. Sloan, N. S. Diffenbaugh and J. L. Bell, 1993.Future climate change and upwelling in the California Current. Geophysical Research Letters, 30(15) 1–4

Solana-Arellano E., Echavarria-Heras H. and S. E. Ibarra-Obando 1997. Leaf size dynamics for *Zostera marina* L. In San Quintin Bay, Mexico: A theoretical study. Estuarine Coastal and Shelf Sciences, 44(3):351–359.

Solana-Arellano E., H. Echavarria-Heras, M. Gallegoz-Marínez and O. Flores-Uzeta, 2004. The role of biotic and abiotic variables in determining demographic processes in an Eelgrass meadow. Bulletin of Southern California Academy of Sciences.103(1):12–19.

Sverdrup H.U., M.W. Johnson and R.H. Fleming 1942. The oceans their physics, chemistry and general biology. Prentice Hall, Inc., Englewood Cliffs N.J. 108 pp.

Tegner M. and P. Dayton 1987. El Niño effects on Southern California kelp communities.

Thayer G.W., W.J. Kenworthy and M.S. Fonseca 1984. The ecology of eelgrass meadows of the Atlantic coast: A community profile. U.S. Fish and Wildlife Service, FWS/OBS-84/02, p. 147.

Titus J.G., 1990. Strategies for adapting to the greenhouse effect. APA J., Summer 1990, 311–323.

Walker D.I. and A.J. McComb. 1992. Seagrass degradation in Australian coastal waters. Marine Pullution Bulletin 25: 191–195.

Watson R.T., M.C. Inyowera and R.H. Moss 1996. Climatic change 1995-Impacts adaptations, and mitigation of climatic change: Scientific-Technical Analysis Contributions of working group *II* to the Second Assessment Report on the Intergovernmental Panel of Climate Change, Cambridge University Press, NY. 878pp.

Wetzel RL. and P.A. Penhale 1983. Production ecology of an eelgrass community in the lower Chesapeake Bay. Marine Technological Society, 17:22–31.

Wigley T.M.L. and S.C.B. Raper, 1987. Thermal expansion of sea water associated with global warming. Nature, 330:127–131.

Zimmerman R.C., R.D. Smith and A. Randall. 1989. Thermal acclimation and whole-plant carbon balance in *Zoster marina* L. (eelgrass). Journal of Experimental Biology and Ecology, 130:93–109.

Zimmerman R.C., J.L. Reguzzoni, S. Wyllie-Echeverria, M. Josselyn and R.S. Alberte. 1991. Assessment of environmental suitability for growth of *Zostera marina* L. (eelgrass) in San Francisco Bay. Aquatic Botany, 39: 353–366.